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DEVELOPMENT OF GONADS AND TRANSFORMATION OF SEX IN THE FROG

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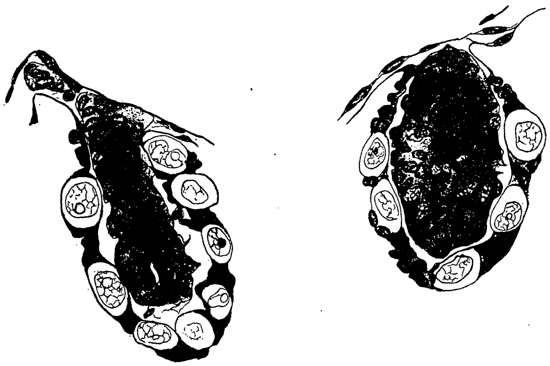
IN the following paper I intend to give a summary of the sexual problems in the frog, as they result from descriptive and analytic research. Richard Hertwig's successful experiments on sex-determination have directed the attention of investigators to this object. From 1911 to 1913 the writer was fortunate enough to have the opportunity of working in Hertwig's laboratory and since then the investigations have been continued at the zoological laboratory of Basle University. The present paper is a brief summary of the development of the sexual characters. In a later publication we hope to explain the experiments on sex-determination and to describe the chromosome cycle.

In the number of this journal for July–August, 1920, Dr. W. W. Swingle has published an interesting study on "Neoteny and the Sexual Problem," and in the February number of the *Journal of Experimental Zoology* the same author has described in greater detail the developmental history of the male gonad of *Rana catesbiana*. In both communications Swingle has disputed the correctness of the work of the Hertwig school. The following explanations may be regarded as a reply to Swingle's critical remarks.

A. THE SEXUAL GLANDS

1. *Morphology of the Undifferentiated Gland.*—The gonad of larvæ 22 mm. in length, just before sex-differentiation takes place, has the following structure. A simple germinal epithelium encloses the central primitive gonad cavity. Five to seven sex cords, budding from the

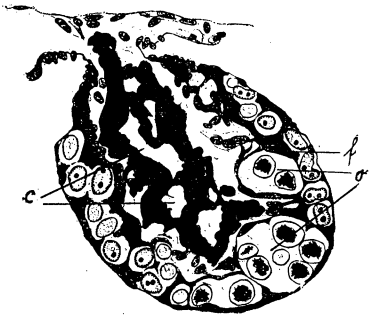
mesonephric blastema at regular distances, fill the cavity as shown in Figs. 1 and 2.



FIGS. 1. AND 2. Transverse sections through the two types of undifferentiated glands. Larvæ 22 mm. total length; 12 days old.

2. *The Ovary.*—The ovary is formed by direct development from the indifferent gonad. In consequence of a rapid increase of the germ cells by mitotic divisions the germinal epithelium thickens. In larvæ of 30–35 mm. total length the germ cells begin to be arranged in ovocysts. After a few simultaneous mitotic divisions the cells of the cysts enter the maturation stages. As Fig. 3 shows, the first cysts are found in the distal part of the gland. Towards the end of the larval period the formation of the oldest ovocysts is disintegrated. Each ovocytis having passed through the stages of pseudoreduction (synizesis, leptotene, pachytene) is surrounded by follicle cells and now enters the second period of growth. The nucleus increases considerably in volume and in the growing protoplasm numerous vitellogen granules appear (Fig. 7, sec. Oc.). Yolk is however not formed normally before the third or fourth season. The sex cords are of greater importance only in the male gonad, forming the testicular interstitium and the rete apparatus—while in the ovary each cord develops into an ovarial sac. As Fig. 1 shows, a little slit may appear already in the undifferentiated gland. More such are found when ovocysts

begin to be formed in the germinal epithelium (Fig. 3, *c*). But during the stage of metamorphosis the slits unite and form only one cavity: the secondary gonad cavity or ovarial sac. In consequence there are in each ovary 5 to 7 sacs, forming the thin gonad endothelium (Fig. 7, I, II).



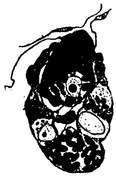


FIG. 3. Section through a young ovary. *C* = secondary gonad cavity. *O* = ovocysts. *F* = follicle cell. Tadpole 38 mm. total length.

FIG. 4. Transverse section through the earliest developmental stage of the testicle. Migration of the germ cells. *sp* = first germ cell in the sex cord (spermatogonia). Tadpole 22 mm. total length; 12 days old.

Characteristics: 1. *Persisting peripheral germinal epithelium.* 2. *First stages of ovocytes in the larval period.* 3. *Occurrence of a second growth period.* 4. *Presence of ovarial sacs.*

Therefore, precocious ripening of germ cells is not my "chief criterion of sex-differentiation," as Swingle says. On the contrary the other three are more characteristic, because they are completely absent in the male line!

3. *The Testis.*—In larvæ 22 mm. in length great differences in the size of the sex cords are found, as seen from a comparison of Figs. 1 and 2. Animals with the stout ones are undergoing transformation into males.

The testis is not formed by direct development from the indifferent gonad. *Its development begins with a change in the position of the germ layers.* The peripheral germinal epithelium having disintegrated, the germ cells cross the primitive gonad cavity and enter the sex cords (Figs. 4 and 5). The follicle cells migrate with the gonia and only the simple peritoneal epithelium remains (Fig. 5).

Shortly after this migration the canaliculi seminalis are formed, at first as irregular slits, but already during metamorphosis they develop into characteristic radiating tubes. At all times they remain connected with the sex cords. These on their part give rise to the rete vasculosum Halleri and the connections with the mesonephros (Vasa efferentia testis).[1]

In the following years the testes grow very slowly until the fourth season, when a rapid increase due to active mitotic divisions of the spermatogonia begins. The spermatic tubes become convoluted; spermatocysts are formed and in the month of July the maturation cycle begins. In August and September the spermatozoa are developed.

In only one case have I found an abortive præspermatogenesis in a three-year-old grass frog (*R. temporaria*). But as Champy has observed, similar degenerating maturation cycles are frequently formed in water frogs (*R. esculenta*) in the second year. According to Swingle precocious ripening of male germ cells in the bull frog (*R. catesbeiana*) already occurs in first year larvæ, and ripe spermatozoa are formed in second year animals.

Characteristics: 1. *Central germinal layer.* 2. *First ripening stages giving rise to functional spermatozoa in the fourth season.* 3. *The maturation divisions directly succeed the pseudoreductional stages.* (There is no second growth period.) 4. *Rete apparatus and Vasa efferentia testis.*

4. *Hermaphrodism.*—It is a strange and interesting fact that the typical development of the testis as just described is rarely observed. Under natural conditions most individuals develop first ovaries which later on are transformed into testes. During this transformation the gonads, showing the characteristics of both sexes, are hermaphroditic; but without exception the female

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[1] Cf. Witschi, 1914.

characters become reduced and mostly disappear completely. In Fig. 6 we have a transverse section through a larval hermaphroditic gland. As in the young ovary (Fig. 3) the distal part contains ovocysts with ovocytes in the synizesis stage, and in the sex cord is found the second gonad cavity or ovarial sac. But the transformation has already begun. The sex cord is more compact than usual and its middle part is penetrated by immigrating germ cells from the basal end of the germinal epithelium. These germ cells after their entrance into the sex cords are to be called spermatogonia.

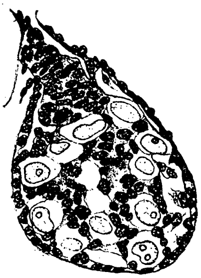

Fig. 5. Cross-section through a young male gonad. Leaved germinal epithelium. All germ cells in the sex cord.

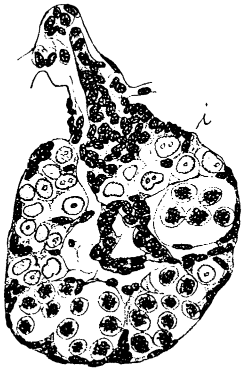

Fig. 6. Transverse section through a larval hermaphroditic gland. Female germinal epithelium; ovarial sac. At (*i*) migrating germ cells.

After the metamorphosis the whole female germinal epithelium undergoes degeneration (only the peritoneum is preserved) while the central testis anlage develops into a normal male gonad.

Sometimes great irregularities are observed. It occurs occasionally that one gonad undergoes the transformation of sex earlier than the other in consequence of which such animals pass through a stage of lateral hermaphrodism. Such cases have often been described and are, I believe, of the greatest interest with regard to the development of somatic sex characters. But even within the same gonad differences can be found. Sometimes the transformation begins at one pole and proceeds continuously to the other. Fig. 7 shows a longitudinal section of such a hermaphroditic gonad. The small testicular part at the posterior end could easily be distinguished macroscopically. The fifth sex cord is almost a normal male one. Numerous spermatogonia are scattered throughout. The slits, which are seen, represent the beginnings of the spermatic tubes. At (*a*) a bridge of tissue is seen, connecting the cord with what is left of the female germinal epithelium. In the fourth cord the transformation has not progressed as far as in the fifth. The center

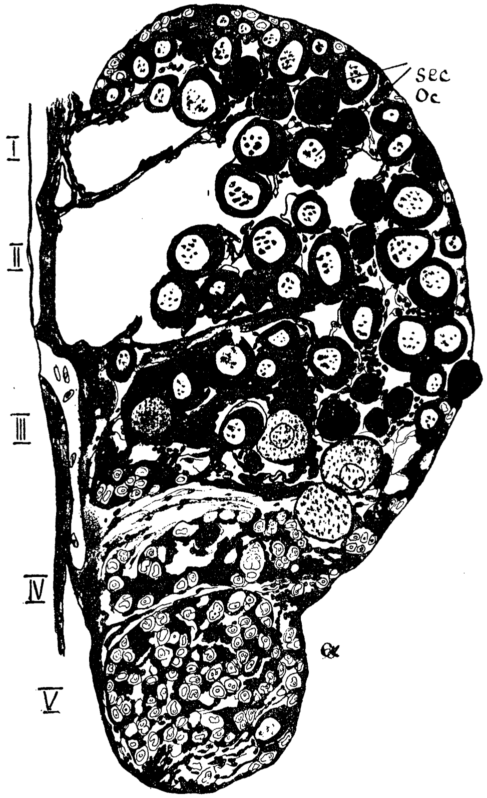

FIG. 7. Longitudinal section through a hermaphroditic gonad. Transformation of sex proceeding from the posterior to the anterior pole. *I–V* = the five sex cords. *sec. oc* = ovocytes in the second growth period.

is occupied by the shrinking ovarial sac with a degenerating egg. The spermatogonia are not numerous but they are already dispersed throughout the wall of the ovarial sac. The germinal epithelium contains a degenerating egg and an ovocyst. The third cord shows the beginning of the process of transformation. It is greatly enlarged, but only a few spermatogonia have migrated into its basal part. Numerous degenerating eggs are scattered over the distal tissue of the sex cord. The germinal epithelium is disintegrating. The second and the first sex cords show the typical proportions of an ovary: wide and thin-walled ovarial sacs and well-developed germinal epithelium. The ovogonia adhere to the peritoneum, the larger eggs projecting inwards. Thus the walls of the sacs are folded on the outside. This preparation is taken from a first year frog, several months after metomorphosis. The transformation of sex in the grass frog often occurs in the second year but likewise is sometimes found in adult animals. Eggs scattered through the testicular tissue have been frequently observed, but ignorance of the development of the gonad has produced the belief that they were derived from spermatogonies. Recently Levy and Swingle claim that these "so-called" eggs only are enlarged ovocyte-like male germ cells; and Swingle believes that "the so-called sexually indifferent or sexually intermediate forms of the Pflüger-Hertwig school are very probably male animals whose germ cells show precocious ripening as far as the pachytene stage" (1920); and "as a consequence of this curtailment of the maturation cycle to the early stages of the process, without exception these writers (Witschi and others), being unable to differentiate male from female, concluded that all frog tadpoles first develop as females, then later half of the female tadpoles must transform into males. . . ." (1921).

It is evident that Swingle has misunderstood our previous communications. In *Rana temporaria* the ovocytes do not always degenerate after the pachytene stages but enter the second growth period (Fig. 7). It is difficult to understand when Swingle says that R. Hertwig, Kuschakewitsch and Witschi "concluded that all frog tadpoles first develop as females." On the contrary I have (1914) described the typical (or direct) development of the testicle as it is to be observed in the alpine *Rana temporaria.* Under optimal conditions of temperature in this variety of the grass frog already after the twelfth day (larvæ 20 to 22 mm. total length) 50 per cent. males are found; in such cultures transformation of sex never occurs.

In his material Swingle has not seen this typical development of the testicle. The described first and second year males are in reality hermaphrodites. His photograph 33, plate 4 (1921) does not show a transverse section through a male but through the female gonad of a first year tadpole, characterized by the ovarial sac (secondary genital cavity) and the peripheral germinal epithelium. Photograph 34 likewise is not taken from a male gonad but from a hermaphroditic one. It shows the same stage of transformation of an ovary into a testicle as Fig. 45 in our publication (1914): representing the gross structure of an ovary, but in the thickened wall of the ovarial sac are several immigrated germ cells (spermatogonia). Photograph 35 illustrates another type of transformation, characterized by an excessive proliferation of the sex cords, as is likewise described in our publication (1914, Fig. 41).

The cytological facts described in great detail by Swingle will be discussed in another communication. They do not alter our view of the significance of the developmental changes.

If there should still remain any doubt in regard to the correctness of my interpretation the following account may help to dispel it.

B. The Somatic Sex Characters

1. *The Müllerian Duct.*—The oviduct first appears as a dense cell cord close to the lateral margin of the kidney. Already in the first sumner the oviducts from the ostium abdominale tubæ to the opening in the cloaca are completely formed. They are thin walled, contain a small lumen, and run straight backwards. In the second year they grow slowly and move away from the ureters. Ordinarily in the third year a large longitudinal growth begins and the duct now becomes folded, as is well known from the anatomy of adult frogs.

In males which show a typical development of the testicles, no Müllerian ducts of any significance are formed. On the other hand, such animals as first develop ovaries and later undergo the transformation of sex, also show regular oviducts; and these continue to grow just up to the time when the transformation of sex begins. *This parallelism in the behavior of the Müllerian ducts and the gonads furnishes definite proof that the "eggs" and "ovocytes," described by the writer, are in fact really eggs and ovocytes and that the transformation of sex is a well-established fact.*

After the transformation of sex, when the ovocytes have disappeared, the Müllerian ducts begin to shrink, but they do not disappear completely, and such reduced oviducts of various sizes are often found in adult male frogs.

Regarding the question of the relations between somatic characters and the gonads, the lateral hermaphrodites furnish most interesting information. The Müllerian ducts are always developed in correlation with the gonad of the same side. Lateral hermaphrodites show always well-developed oviducts on the ovarial side and smaller ones on the testicular side. The correlation is therefore independent of the action of hormones.

2. *The Vesicula Seminalis and the Thumb Cushion.*—The male somatic characters appear chiefly in the second year and always develop symmetrically, in lateral her-

maphrodites, both sides depending from the first formed testicle. They seem, however, not to be influenced by internal secretions, as all experiments gave negative results. We will not enter here into this much discussed problem, but refer the reader to our publication on hermaphrodism.

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